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Germination and Dormancy in Seeds of *Sapium sebiferum* (Chinese Tallow Tree)

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ABSTRACT

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Glasshouse studies were conducted to determine seed germination of *Sapium sebiferum* (L.) Roxb. (Chinese tallow tree), an exotic woody invader from Asia. This species has spread throughout the southeastern U.S. during the past several decades. This tree invades native coastal prairie and abandoned agricultural areas to create monospecific stands within about 20–25 years. The tree is difficult to control because of high fecundity, root- and stump-sprouting, and few pests or pathogens in the U.S. Scarcity of data on seed dormancy and germination make it difficult to formulate management plans. We planted seeds collected over a 7-year period and found that maximum germination was in January–February and after a storage period of two years; germination was reduced to only 3% by the seventh year of storage. There was significant geographical variation in the proportion of germinated seeds and the rate of germination. Seeds from Florida gave the highest (52%) germination success and germination rate while those from South Carolina had the lowest (6%) germination success and rate.

ADDITIONAL INDEX WORDS: *Exotic species, Chinese tallow tree, seed germination, seed dormancy.*

INTRODUCTION

The Chinese tallow tree [*Sapium sebiferum* (L.) Roxb.; Euphorbiaceae] is a subtropical, deciduous tree native to China and cultivated there for production of soap and candles from the waxy seed coat, fuel from the wood pulp, drying oil from seed kernels, black dye from leaves, and protein meal from seed kernels (POTTS, 1946; SCHELD *et al.,* 1984). *S. sebiferum* has been introduced worldwide for both economic and ornamental purposes. As a result, naturalized populations of tallow occur throughout the southeastern U.S. and are particularly abundant along the coast of the Gulf of Mexico (BRUCE *et al.,* 1997).

S. sebiferum possesses traits of a typical invading species, including tolerance for a wide variety of soil types, rapid growth, precocity, high fecundity, and effective seed dispersal (BRUCE *et al.,* 1997). The proportion of seeds that germinated was similar, but growth rate of seedlings was higher than for native tree species (BRUCE, 1993; HALL, 1993). *S. sebiferum* grows rapidly, attaining a height of 2.8 m within two years after germination (SCHELD and COWLES, 1981), and half of the population may become reproductive by the third year of their life (SCHELD *et al.,* 1984). In China, seed yield peaked near 11.9 kg/yr for trees 25–30 years old and then declined to about 5.9 kg/yr for 50-year-old trees (LIN *et al.,* 1958). On the Texas coastal prairie, seed production surpassed 4,484 kg $ha^{-1}yr^{-1}$ (SCHELD *et al.,* 1980), and seed viability was as high as 88–98% (BRUCE, 1993).

In Texas, *S. sebiferum* rapidly invades remnant areas of abandoned agricultural land and native coastal prairie (comprised of little bluestem [*Schizachyrium scoparium*], brownseed [*Paspalum plicatum*], and Indian grass [*Sorgastrum nutans*]; SMEINS *et al.,* 1991), transforming this vegetation to woody stands containing 98% tallow within 20–25 years (BRUCE *et al.,* 1995). The rate of invasion of coastal prairie is so rapid that coverage by *S. sebiferum* for Galveston County south of Houston increased from approximately 2% of land area in 1970 to 16% in 1990 and is predicted to be >30% by the year 2000 (SMITH, 1991). In addition, net primary productivity of monospecific stands of tallow was higher than for native coastal prairie, and soil under these stands had higher concentrations of P, K, NO_3-N, Zn, Mn, and Fe, and lower concentrations of Mg and Na (HARCOMBE *et al.,* 1993; CAMERON and SPENCER, 1989).

Because of these traits, along with their suspected long-term viability in the seed bank, *S. sebiferum* has become a serious threat for maintenance of native prairie and wetland habitats in the southeastern U.S. (JUBINSKY and ANDERSON, 1996; BRUCE *et al.,* 1997). Accordingly, details of the reproductive biology of this exotic species are needed to determine how long areas must be monitored after removal of trees for re-invasion or re-growth. To provide such information, we measured the germination success and germination rate for *S. sebiferum* seeds collected from localities in the southeast-

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Table 1. *Percent germination (mean ± SE) of* Sapium sebiferum *seeds of different ages after 120 days of planting on different dates.*

Year Seeds Collected	Age (yrs) of Seeds	Date of Planting: Nov 2	Nov 30	Jan 2	Feb 1	Mar 6	Apr 5
1981	7	0	0	12 ± 3.7	6 ± 2.5	2 ± 2.0	0
1983	5	18 ± 8.0	48 ± 5.8	52 ± 13.6	36 ± 22.3	20 ± 3.2	20 ± 5.5
1984	4	36 ± 9.3	60 ± 8.4	64 ± 5.1	80 ± 4.5	40 ± 5.5	28 ± 7.3
1986	2	44 ± 9.3	82 ± 3.7	94 ± 2.5	84 ± 4.0	76 ± 7.5	46 ± 7.5
1988	0	8 ± 5.8	40 ± 4.5	66 ± 6.8	92 ± 5.8	40 ± 8.4	14 ± 4.0

ern U.S. and its native range in Taiwan. We also determined the effect of length of storage on germination success. While not absolutely comparable, length of storage was taken to be representative of the length of time in the seed bank.

METHODS

Our research was conducted at the University of Houston, Houston, Texas, and the University of Houston Coastal Center, 56 km southeast of Houston, Texas. The first experiment determined the effect of month of planting and time of storage on germination success for 0–7 year-old seeds. Seeds used had been collected from a single mature tree (Tree #57) at the Coastal Center during the fall of 1981, 1983, 1984, 1986, and 1988. This tree had been selected because it had excellent annual biomass production, a heavy seed yield during each of these years, and to minimize variation in germination success because of differences among trees. Seeds were stored dry at 4°C (1981) or 0°C (remaining years) until planted. Five replicates from each year were established on 2 November 1988; each replicate consisted of 10 seeds planted at a depth of 4 cm in individual dibble tubes (Ray Leach Conetainers®) containing MetroMix 200® planting media (to which 34 g of gypsum was added per 1 m^3 of soil mix; a total of 50 seeds were planted from each year). Thereafter, seeds from each year were planted at approximately monthly intervals with the last planting on 5 April 1989. Each replicate consisting of 10 dibble tubes was positioned randomly in trays that were maintained in a glasshouse at the Coastal Center under natural temperature and photoperiod. Tubes were watered regularly to maintain soil moisture, but no nutrients were added. Germination was determined with daily observations by the appearance of the epicotyl aboveground for the seed in each dibble tube. The number of seeds (out of 10) that germinated in each replicate was assessed 120 days after planting, and the mean percent of seeds that germinated for the five replicates was computed for each month (November–April) and each year (1981–1988).

A second experiment was designed to analyze geographic variation in total proportion of seeds that germinated and cumulative number of seeds that germinated over time. Seeds were obtained from 126 trees in May 1982. These accessions were from 10 localities in the southeastern U.S. (Houston, Texas [3 localities]; College Station, Texas [3 localities]; near Jacksonville, Florida; near Savannah, Georgia; Louisiana; and between Charleston and Georgetown, South Carolina) and from Taiwan. Seeds were stored dry at 0°C. Fourteen seeds from each accession were planted from 6–8 February 1988 (determined to be the optimal month for germination from the experiment described above) at a depth of 4 cm in individual dibble tubes containing MetroMedia 200®. Dibble tubes were placed in trays in a glasshouse at the University of Houston under natural temperature and photoperiod. Tubes were watered regularly to maintain soil moisture, but no nutrients were added. The date of germination of the seed in each dibble tube was recorded from weekly observations between 12 March and 30 April or 7 May (*i.e.,* the spring sprouting season). The proportion of seeds that germinated (out of 14 planted) was computed for each accession. In addition, the survival of each seedling to the end of the first growing season in the glasshouse was recorded on 3 November, and the proportion surviving (out of 14 planted) was computed for each accession. Data from College Station and Louisiana were not included in our analyses because too few seeds were collected, and the three locations from Houston were considered as a single locality for analyses, resulting in a final sample size of 122 trees.

An arcsine transformation was applied to data expressed as a percent. A two-way analysis of variance (ANOVA) was used to determine the effect of date of planting and year of seed collection on percent of seeds that germinated. While both storage time and year of harvest may affect germination, the effect of the former is more pronounced. Kendall's Coefficient of Concordance (W) was used to determine whether the temporal pattern of germination was similar (*i.e.,* concordant) among years. Percent of *S. sebiferum* seeds that germinated on each date of planting were ranked within each year for this analysis and significance of W was tested with a Chi-square (ZAR, 1996). Differences among localities in total percent of seeds that germinated after 120 days, and survival of seedlings to the end of their first year were tested with ANOVA. The rate of germination of seeds from each locality was determined by computing a germination index (KHAN and UNGAR, 1984). This index computed the germination velocity as $\sigma G/t$, where G = percentage of seeds germinated at 7-day intervals, t = total germination period (49 days). The maximum possible value for this index was 14.3

Table 2. *Analysis of variance table for the percent of* Sapium sebiferum *seeds that germinated on different planting dates (months) and from different collection years (years).*

Variable	df	Mean Square	F-value	P
Month	5	3800.05	21.9	<0.0001
Year	4	12019.28	69.2	<0.0001
Month * Year	20	477.80	2.8	<0.0004
Residual	120	173.73		

Table 3. *Total percent germination of seeds, germination index of seeds, and survival of seedlings (mean ± SE) of* Sapium sebiferum *seeds collected from various localities. n = number of trees sampled from each locality. Values with different superscript letters are significantly different according to Fisher's PLSD test.*

Locality	n	°N latitude	Total Percent Germinated	Percent Survival to End of Growing Season	Germination Index
Houston	53	29.46	24.3 ± 2.7[a]	14.3 ± 2.1[a]	0.022 ± 0.003[a]
Taiwan	36	23.30	28.8 ± 3.3[a]	16.3 ± 3.1[a]	0.019 ± 0.002[a]
Florida	9	29.40	52.4 ± 5.9[b]	16.7 ± 5.9[a]	0.041 ± 0.006[b]
Georgia	9	33.11	30.9 ± 6.3[a]	11.9 ± 3.9[a]	0.024 ± 0.006[a]
South Carolina	15	32.47	5.7 ± 3.1[c]	0.9 ± 0.7[b]	0.003 ± 0.001[c]
Total	122		25.9 ± 1.9	13.22 ± 1.4	0.020 ± 0.002

if all 14 seeds germinated each day (700/49). Germination rate was transformed with log+1.0 and analyzed with ANOVA.

RESULTS

A significantly higher proportion of *S. sebiferum* seeds germinated in January and February (average: 58–59%) with lower percentages germinating in late fall (average: 21–46%) and early spring (average: 22–36%; Tables 1, 2). Kendall's Coefficient of Concordance showed that there was a significant association in the percentage of seeds that germinated on each date of planting among the years seeds were collected ($W = 0.864$; $\chi^2 = 21.6$; df = 4; $P < 0.001$).

The length of time that *S. sebiferum* seeds were stored significantly affected their germination (Tables 1, 2). Germination success was highest for two-year old seeds, and was lower for seeds collected during the year of planting (1988). Germination of seeds began decreasing in years 4–5 and was quite low by 7 years. There was a significant planting date-year interaction (Table 2) because the highest and lowest germination rates did not always coincide during the same month in all years. For example, percent of seeds that germinated peaked in January during 1981, 1983, and 1986, but in February during 1984 and 1988.

There was significant geographic variation in the total proportion of *S. sebiferum* seeds that germinated. Germination success of seeds from Florida was the highest and from South Carolina the lowest (Tables 3, 4). Trees from Houston, Taiwan, and Georgia had intermediate, but similar, total proportion of seeds that germinated. There was a significant difference in the germination index among localities (Tables 3, 5). Germination rate was significantly higher for Florida and was significantly slower for seeds from South Carolina. Rates of germination for seeds from Houston, Taiwan, and Georgia were intermediate. Survival of seedlings in the glasshouse from South Carolina was significantly lower than that from all other localities (Tables 3, 6).

DISCUSSION

Highest germination success of *S. sebiferum* seeds occurred during January and February, whereas lowest germination was during late fall and early spring regardless of the year. Maximum germination success of *S. sebiferum* during winter would be advantageous in this habitat for several reasons. Herbaceous ground cover along the Gulf coast is minimum during winter because annual plants and standing live biomass of perennial herbaceous vegetation dies back leaving only standing dead vegetation (HARCOMBE *et al.,* 1993). In addition, most trees on the Texas coastal prairie are deciduous. The result is that there is little competition from other vegetation for sunlight and nutrients during winter. Finally, insect seed-predators are inactive during winter, and abundance of granivorous small mammals and birds is low (CAMERON, unpublished; CAMERON, 1977).

Time of storage affected germination success, with maximum germination after seeds were kept in cold-storage for 2 years. However, continued storage resulted in progressive deterioration of the proportion of seeds that germinated. Because *S. sebiferum* seeds required a period of time under cold temperatures to achieve maximum germination success, winter temperatures in the field would affect germination success and geographic distribution or among-year abundance of this exotic species. Furthermore, these results show that seeds in the soil could be viable for at least 5 years after they had been shed. Even if only 3% of seeds germinated after 7 years, a resurgence in abundance of *S. sebiferum* could result in areas from which the species had been removed, suggesting that land managers must monitor areas for at least this long after initiation of control against this species (also see JUBINSKY and ANDERSON 1996).

There was significant geographic variation in the proportion of *S. sebiferum* seeds that germinated, germination rate, and seedlings that lived to the end of the growing season. *S. sebiferum* from Florida had the highest and *S. sebiferum* from South Carolina the lowest germination success and germi-

Table 4. *Analysis of variance table for the percent of* Sapium sebiferum *seeds that germinated from different localities.*

Variable	df	Mean Square	F-value	P
Locality	4	2445.56	10.4	<0.0001
Residual	117	235.82		

Table 5. *Analysis of variance table for the germination index of* S. sebiferum *seeds from different localities.*

Variable	df	Mean Square	F-value	P
Locality	4	3.0×10^{-4}	8.5	<0.0001
Residual	116	4.72×10^{-5}		

Table 6. *Analysis of variance table for the percent of* Sapium sebiferum *seedlings that germinated from different localities.*

Variable	df	Mean Square	F-value	P
Locality	4	899.72	4.3	<0.003
Residual	116	211.65		

nation rate. *S. sebiferum* from the other localities, including the native range in Taiwan, were intermediate in value, except for seedling survival where there was no difference between these localities and Florida. This was not strictly a latitudinal gradient because the proportion of seeds that germinated from trees in Houston was half that from trees in Florida even though they were at nearly the same latitude. On the other hand, seeds from the most northerly locality, South Carolina, exhibited the lowest percent germination. Local factors, principally edaphic or microclimatic, as well as genetic differences among localities could have affected the time of maturation of tallow trees. On the other hand, since all collections were made during May 1982, different geographic localities may not have had trees at the same level of reproductive maturity.

Few other data are available on germination success or the length of time that *S. sebiferum* seeds remain viable in the soil bank. HARPER (1995) found that germination success was 0–10% for *S. sebiferum* seeds in mature floodplain forests in Louisiana, with 10–15% of seeds viable after 1 year in the soil. The germination success of *S. sebiferum* seeds that we found in the glasshouse was much lower (average 26%) than the germination success of seeds of tree species native to the coastal prairie, *e.g.,* loblolly pine (*Pinus taeda*), water oak (*Quercus nigra*), hackberry (*Celtis laevigata*), and American elm (*Ulmus americana*) in both laboratory and glasshouse trials (Table 7). However, BRUCE (1993) planted seeds from *S. sebiferum* and these four species in field plots containing coastal prairie vegetation, and showed, when corrected for viability, there was no difference among species in the proportion of seeds that germinated. *S. sebiferum* seeds remained viable in storage for as long as the native species except water oak whose viability decreased substantially after 6 months in storage.

Germination success and retention of viability in the seed bank for *S. sebiferum* was similar to that of native tree species. The successful invasion and subsequent domination of the coastal prairie habitat by this exotic species, therefore, may be less a result of differential seed characteristics in comparison to native woody species than of rapid growth rate exhibited by the seedlings (BRUCE, 1993). Average height of *S. sebiferum* seedlings after one growing season was 22 cm, compared to 9 cm, 12 cm, and 9 cm for native loblolly pine, water oak, and hackberry, respectively (BRUCE, 1993). In addition, *S. sebiferum* seedlings may be better able to withstand the shrink-swell nature of the clay soil on the coastal prairie than native species (BRUCE, 1993). This physiological characteristic may enable the Chinese tallow tree to obtain a foothold in the prairie and attain dominance in a short time.

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Table 7. *Amount of time that seeds remained viable and proportion of seeds that germinated for several native woody species that grow in riparian zones on the Texas coastal prairie (Schopmeyer, 1974).*

	Seed Viability		Germination Trials		
Tree Species	Age (yrs)	Storage Temp. °C	Percent Germination	Time Tested (days)	Experiment Temp. °C
Celtis laevigata	5.5	5	55	60	30 day; 20 night
Pinus taeda	9+	unknown	90	30	22 day; 22 night
Quercus nigra	<0.5	0 to 4	60–94	52–73	43 day; 22 night
Ulmus americana	15	−15	64	14–60	30 day; 20 night

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